Dispersion and habitat preference of the Water vole (Arvicola terrestris) on the River Thames

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Abstract

Investigated the dispersion of water voles (Arvicola terrestris) over a two year period on a 1.6 km stretch of the River Thames near Oxford, England. Dispersion was significantly clumped, most pronounced for adult females, followed by juveniles and least for adult males. The river bank was divided in 32 50-metre sections and data on the vegetation and physical features of each section were analysed with the frequency of water vole catches in each section to determine habitat preferences. Water vole catches were positively correlated with water depth, Urtica, Phragmites, and short unidentified grasses and negatively correlated with bank height, bank depth, Polygonum, Phalaris, Sparganium, Juncus. The favoured plants all provided food and also cover in the case of Phragmites and Urtica. Shallow water was avoided even though its associated emergent macrophytes provided cover. Deep water may allow the water voles to escape predation by diving and swimming away.

Introduction

The water vole (*Arvicola terrestris* L.) has a wide Palaearctic distribution. In Europe it is often found away from water but the British populations are, with few exceptions, almost completely restricted to aquatic habitats (BOYCE 1991).

Most previous investigations of the water vole's habitat have been conducted in Europe and have been largely qualitative emphasising the importance of food plants (WIJNGAAR-DEN 1954; ZEJDA and ZAPLETAL 1969; GAISLER and ZEJDA (1974). More recently, LAWTON and WOODROFFE (1991) conducted a quantitative survey of the habitat of water voles on rivers in the North Yorkshire moors where there were many gaps in their distribution. They found that areas inhabited by water voles were characterised by a high percentage of grass, steep bank angles and relatively high layering of the vegetation. Other sites containing apparently suitable habitat were unoccupied by water voles due to their isolation or mink *Mustela vison* predation.

This study used similar quantitative methods in an intensive investigation of the water vole's dispersion on a large, lowland river in Britain, where mink were absent, and attempted to identify the major biotic and abiotic variables correlated with the water voles' pattern of dispersion.

A nation-wide survey suggested a long-term decline of water vole populations in Britain this century, possibly associated with habitat changes and the spread of mink (JEFFERIES et al. 1989). Therefore it is important to identify the key features which determine the habitat preference of water voles.

The study area

The study was conducted at the Oxford University Field Station on the River Thames extending from the foot of Wytham Wood, near the entry of the Evenlode to the Thames, to the origin of Seacourt Stream (Fig. 1). The study concentrated on three fields with different forms of land use: Field A was



Fig. 1. The location of the three fields A, B, and C which formed the study area on the River Thames, north of Wytham Wood. The dashed line indicates the 61 m a. s. l. contour line

sown to grass in 1970 with several varieties of Perennial Rye grass and White Clover, and was used for silage and grazing; Field B was planted with Spring Barley each year; and Field C was an old permanent pasture used for grazing and hay-making. These forms of land use are fairly representative of the Upper Thames catchment (THAMES CONSERVANCY 1969) and have not changed greatly since the 18th century (GRAYSON and JONES 1955). The vegetation on the river bank is rather different from that found in the fields because, in addition to the riparian influence, it is never cut or harvested. However, it is grazed by cattle, with heaviest grazing in Field C and lightest in Field B which is only grazed for a very short period once the barley and straw have been harvested. The bank had a variety of plants, characterised by perennial dicotyledons (e.g. Stinging Nettle *Urtica dioica*, Creeping Thistle *Cirsium arvense* and Great Hairy Willow Herb *Epilobium hirsutum*) and emergent macrophytes (e.g. Soft Rush *Juncus effusus*, Bur-Reed *Sparganium erectum*, Common Reed *Phragmites communis*, Sweet Reedgrass *Glyceria maxima* and Reed Canary-grass *Phalaris arundinacea*).

Material and methods

Water vole numbers and distribution

Information on the distribution of water voles along the study area was obtained from a trapping programme. The study area was divided into 32 sections of river bank, each 50 m long. The number of individual water voles caught in each of these sections and the total number of water vole catches (including recaptures) was calculated for different periods within the year and for different age and sex groups. The three fields (A, B, and C) were not trapped with equal intensity because of the problems caused by the occasional presence of grazing cattle. Therefore the number of water vole catches in Fields A and C was corrected (× 1.45 and × 1.36 respectively) to reflect equal trapping intensity.

Water voles were caught in live traps made according to STODDART's (1970) design, with slight modifications, and were baited with apple. The traps were placed 20–25 m apart, so there were 2–3 traps in each section of the river bank, and every effort was made to place them in runways or other sites of water vole activity. At each monthly trapping session the position of individual traps was accurately located (to the nearest metre) by pacing between the traps to markers on the river bank (fences, trees, bushes, etc). Initial experiments showed that prebaiting was not necessary and traps were left in position for one day (February to November 1975) or two days (December 1975 to November 1976) each month. With slight variations in the numbers of traps available, and thus intertrap distances, traps were seldom placed in exactly the same position in successive trapping sessions.

In this discussion, a juvenile water vole refers to one born in the calendar year under discussion (i.e. an animal of the year) and an adult is a water vole which has survived at least one winter. Thus, at the end of December, all juveniles surviving to the following January become adults.

Physical features of the river bank

In June 1977, when water levels were near to normal, the bank profile was measured at 20 m intervals. A vertical, graduated pole was placed at the water's edge and the horizontal distance to the bank at 10 cm intervals up the pole was recorded. Similarly by floating a graduated plank attached to the

vertical pole, the depth of water at 10 cm intervals perpendicular to the bank was recorded. These measurements were plotted on graph paper and the following parameters obtained (Fig. 2): A: bank height; B: bank depth (distance from the vertical at maximum height; C: depth of water at 50 cm; D: depth of water at 100 cm; E: bank gradient (height/depth).

Surface soil samples, 10 cm deep, were taken at 20 m intervals on the river bank, 1 m from the water's edge. These were later hand textured and ranked from clay (5) to gravel (1). The aspect of the bank and the curvature of the bank (deviation from the mean direction of flow for 50 m upstream) were obtained from large-scale maps of the study area.



Fig. 2. Measurements taken from bank profiles in the study area: A = bank height; B = bank depth; C = water depth at 50 cm; D = water depth at 100 cm; E = bank gradient (A/B)

Vegetation

The vegetation parameters used in this analysis were obtained from a survey in August 1977 when most of the species (particularly the grasses) were still flowering and so could be readily identified. A quadrat extending 1 m from the water's edge and 0.2 m wide was located at 20 m intervals along the river bank (n = 78) and each species in the quadrat was given an importance value (1–10) based on 10 % intervals of its estimated percentage of coverage. Although this assessment of vegetation was relatively crude, it allowed a large number of sites to be sampled and provided some improvement on simple presence or absence data (LAMBERT and DALE 1964; WALKER 1974).

Data analysis

To test whether the distribution of water vole captures in the study area was random or clumped, Morisita's Index of dispersion, I_{δ} was calculated. The significance of departures from random (1.00) was determined using tables in SOUTHWOOD (1966).

To determine which environmental variables (or combinations of variables) best "explained" the distribution of the water vole on the study area (i.e. accounted for most of the variance from a mean value) various statistical methods were used. It must be emphasised that this type of analysis does not prove a cause and effect relationship for it is quite possible that a correlated variable is either merely spurious or is itself correlated with some other key variable. The results from these analyses must be used with biological reasoning.

First a correlation matrix was calculated to investigate the effects of individual variables on the water vole's dispersion. To investigate the effects of several variables, multivariate methods (multiple correlation, multiple regression, factor analysis) were then used. Two methods of factor analysis, Principal Component Analysis (PCA) and (Classical) Principal Factor Analysis (PFA) differing in their underlying models, were used. Since PCA, in particular, is very dependent on the variance of the original variables, it is important that these should be of the same order of magnitude, so all were standardised (mean = 0, variance = 1) as recommended by HARMAN (1976).

Results

The trapping programme produced two types of information: the distribution of individually marked animals, where the presence of an individual in a section is recorded only once; and the distribution of all catches, including recaptures. The former reduces the effect of repeated recaptures of "trap-happy" individuals but gives equal weighting to both an individual's core area and fringe areas, where it may be found only sporadically. The total number of catches clearly indicates sections where individuals are caught repeatedly. In practice both provided data which were strongly correlated (adult males: r = 0.81; adult females: r = 0.77; juveniles: r = 0.62) and the following analysis is restricted to the distribution of total catches (Fig. 3). In both cases, an underlying assumption is that the pattern of catches represents the pattern of activity and distribution – this is considered further in the discussion.



Fig. 3. The total numbers of adult male, adult female and juvenile water voles caught on the study area (corrected to equivalent trapping effort) in each 50 m section of the river bank

Dispersion of water voles

In the three fields under investigation, 815 catches of water voles were made in 2796 trapnights. The distribution of these catches was clearly non-uniform (Fig. 3) and Morisita's index of dispersion (Tab. 1) showed significant clumping for all categories but least for adult males and most for adult females with juvenile males and females being intermediate.

Other rodents were virtually absent in this habitat, a brown rat *Rattus norvegicus* was caught only once during the entire trapping programme. Stoats *Mustela erminea* and weasels *M. nivalis* were occasionally seen but never caught, and mink *M. vison* were never recorded in the study area.

The correlation of catches in the 32 positions between adult males and females was significant but low (r = 0.413, P < 0.05) and the catches of adult males were not significantly correlated with those of

Table 1. Dispersion of water voles on the River Thames

Water vole category	Morisita's Ið
Total numbers	1.09*
Adult Males	1.12**
Adult Females	1.36**
Juvenile Males	1.28**
Juvenile Females	1.20**

P. F. Woodall

juvenile males or juvenile females (r = 0.084, 0.190, P > 0.10 respectively). However, catches of adult females were significantly correlated with those of juvenile males and females (r = 0.402, 0.392, P < 0.05) and catches of juvenile males and juvenile females were strongly correlated with one another (r = 0.684, P < 0.001). In subsequent analyses juvenile males and females are lumped together.

Negative correlations were found between Morisita's Index of Dispersion and the estimated Mean Number Alive (WOODALL 1978) when total water vole catches over five periods (Feb.-May 1975, June-Oct. 1975, Nov. 1975–Feb. 1976, Mar.-May 1976, June-Aug. 1976) were examined (r = 0.839, n = 5, 0.05 < P < 0.1). This may suggest that at higher population densities the water voles are more evenly dispersed but this result is complicated by seasonal factors and changes in the population structure with increasing proportions of juveniles at high densities.

Univariate analysis of habitat variables

Several variables reflecting physical dimensions of the environment showed significant correlations with water vole catches (Fig. 4, Tab. 2). Water depth at 100 cm from the bank was positively correlated with all categories of water voles, significantly so for total catches and adult females. Bank height was negatively correlated with catches of adult females and bank depth showed significant negative correlations with total catches and catches of adult males. Bank deviation showed a significant negative correlation with catches of adult females, this is difficult to explain but may reflect an association with some emergent plants (*Juncus effusus*, etc.).



Fig. 4. Mean physical parameters (Bank height [A], Bank depth [B] and Water Depth at 100 cm [D]) at each section along the river bank

The vegetation on the river bank was quite diverse and, even after excluding 16 species which had total scores of < 10 (summed over the 32 positions), 18 species remained. One of these "species" consisted of grasses which had been grazed short to give a lawn-like appearance and which could not be identified to species. Hereafter it is referred to as Gramineae indet. The distribution of eight plants showed significant correlations with the distribution of water vole catches (Tab. 3, Figs. 5, 6). *Urtica dioica* and Gramineae indet. were positively correlated with total catches and those of adult males and females,

164

River bank	Water vole					
	Total No.	Ad.Male	Ad.Female	Juv.		
Bank height	-0.210	0.067	-0.340+	-0.164		
Bank depth	-0.358*	-0.387*	-0.286	-0.132		
Bank gradient	0.149	0.289	0.037	0.024		
Depth at 50 cm	0.313+	0.288	0.188	0.220		
Depth at 100 cm	0.429*	0.308+	0.349*	0.285		
Soil texture	0.195	0.084	0.156	0.179		
Aspect	0.023	0.049	0.207	-0.193		
Deviation	-0.278	-0.028	-0.399*	-0.166		

Table 2. Correlations between the distribution of water voles and physical features of the river bank on the Thames

Table 3. Correlations between the distribution of plant species and water voles on the River Thames

Plant species	Water vole				
	Total No.	Ad.Male	Ad.Female	Juv.	
Urtica dioica	0.505**	0.453**	0.417*	0.251	
Polygonum amphibium	-0.295^{+}	-0.369*	-0.130	-0.169	
Rumex conglomeratus	-0.003	-0.041	0.271	-0.230	
Erysimum cheiranthoides	0.116	0.209	0.184	-0.116	
Filipendula ulmaria	-0.081	0.040	-0.105	-0.100	
Epilobium hirsutum	0.137	0.074	0.006	0.213	
Scrophularia auriculata	0.221	0.265	0.082	0.150	
Cirsium arvense	-0.100	0.256	-0.051	-0.374*	
Juncus effusus	-0.142	0.097	-0.316^{+}	-0.072	
Sparganium erectum	-0.302^{+}	-0.203	-0.389*	-0.075	
Ĝlyceria maxima	0.097	-0.145	0.212	0.199	
Dactylis glomerata	-0.042	0.049	-0.021	-0.109	
Arrhenatherum elatius	-0.182	0.033	-0.259	-0.154	
Holcus lanatus	-0.180	-0.114	-0.248	-0.035	
Phalaris arundinacea	-0.336+	-0.381*	-0.271	-0.107	
Phelum pratense	-0.197	-0.279	-0.158	-0.016	
Phragmites communis	0.459**	0.249	0.299+	0.445**	
Gramineae indet.	0.362*	0.372*	0.551**	-0.102	

Phragmites communis was positively correlated with total catches and those of adult females and juveniles (Fig. 5).

Polygonum amphibium and Phalaris arundinacea were negatively correlated with total catches and those of adult males. Sparganium erectum was negatively correlated with total catches and those of adult females, Juncus effusus was negatively correlated with adult female catches and Cirsium arvense was negatively correlated with juvenile catches (Fig. 6).

Multivariate analysis of habitat variables

Multivariate analysis was used to investigate and display some of the interactions between variables. In view of the crude nature of some of the variables, this is used not as a rigorous statistical analysis but rather as an investigative tool.

The proportion of variance in the distribution of water vole catches "explained" by the



Fig. 5. Mean importance values (see text) at each section along the river bank for some plant species (*Urtica dioica, Phragmites communis*, Grass spp.) which showed significant positive correlations with water vole catches



Fig. 6. Mean importance values (see text) at each section along the river bank for some plant species (Polygonum amphibium, Juncus effusus, Sparganium erectum, Phalaris arundinacea) which showed significant negative associations with water vole catches

12 environmental variables with significant univariate correlations was indicated by the square of the multiple correlation co-efficient (R^2): 0.55 for adult males; 0.79 for adult females and 0.64 for juveniles. These results correspond with the results of Morisita's index of dispersion showing adult females have the most clumped dispersion (thus more readily explained by environmental variables) while adult males have the least clumped dispersion and so are less explicable by the environmental variables.

Since many of the environmental variables were strongly correlated with one another, stepwise multiple regression did not extract many of the variables shown to be significant by univariate analysis, so Principal Component Analysis was used to reduce the variables to one or more factors which were orthogonal (i.e. uncorrelated).



Fig. 7. The relative association of water vole numbers and vegetation and physical parameters on two factors generated by Principal Factor Analysis. 1 = adult male water voles; 2 = adult female water voles; 3 = juvenile water voles; 4 = bank height; 5 = bank depth; 6 = bank gradient; 7 = water depth at 50 cm; 8 = water depth at 100 cm; 9 = deviation of river bank; 10 = Urtica dioica; 11 = Polygonum amphibium; 12 = Cirsium arvense; 13 = Juncus effusus; 14 = Sparganium erectum; 15 = Phalaris arundinacea; 16 = Phragmites communis; 17 = Gramineae indet

Including only those variables with significant correlations with water vole numbers, both PCA und PFA (with varimax rotation and 1 factor fixed) gave similar results (Fig. 7). Water vole numbers, especially adult males and females, had high positive loadings on Factor 1 together with water depth at 50 and 100 cm, and *Phragmites communis*. Variables with strong negative loadings on Factor 1 included Bank Depth, *Polygonum, Sparganium* and *Phalaris*. This factor seems to represent a trend from deep water and associated *Phragmites communis* to a large bank depth, shallow water and its associated plants.

Female water voles, and to a lesser extent juveniles, had high negative loadings on Factor 2, together with *Urtica* and short Gramineae indet. Bank height, bank gradient, deviation, *Cirsium*, and *Juncus* had high positive loadings on Factor 2. This factor seems to represent a trend from high banks, and steep gradients to lower banks with *Urtica* and short Gramineae indet.

Discussion

This study assumes that, with equal trapping effort, the varying number of water voles caught in different parts of the study area reflected varying intensities of utilization of the area by water voles. Trapping is not the best method of investigating an animal's spatial activities, since it interrupts the activity and may preferentially sample certain portions of the population. However, other methods of recording activity also have drawbacks and without using radio telemetry (which usually limits sample size), trapping seems to be a practical if not ideal alternative (GRANT and MORRIS 1971). Other measures of water vole activity (holes in the river bank, latrines, food remains) were all associated with areas where water voles were caught frequently and areas where water voles were seldom caught lacked these signs of their activity. Therefore, the trapping results seem to have provided a useful measure of the water vole's dispersion patterns and activity.

Dispersion

The dispersion of water voles in the study area was clumped, significantly different from a random pattern. There was some indication that their dispersion became more random and

less clumped as the population density increased and similar results were found by GRANT and MORRIS (1971) for *Microtus pennsylvanicus*. However, this result is confounded by the fact that at high densities much of the population was made up of juveniles that may show less clumping than adults. Sample sizes were inadequate to analyse adults alone at different seasons.

These results differ from those of STODDART (1970) who found that water voles were evenly distributed along a stream in Scotland with no indication of clumping. This was probably due to a much more uniform habitat. They also differ from LAWTON and WOODROFFE's (1991) study in the North Yorkshire Moors National Park where they found major gaps in the distribution of water voles along the rivers, explained by unsuitable habitat, mink predation and isolation. In this study on the Thames no section was completely avoided (Fig. 3) although some areas were much more heavily used than others. The possible reasons for this are considered below.

Adult males showed less habitat selectivity than females: their dispersion was less clumped and less of the variance of their capture sites could be accounted for by the environmental variables. This is consistent with the significantly larger home ranges of males (STODDART 1970; BOYCE 1991) particularly in summer (WOODALL 1978) which means that they move over a wider range of habitats than do the females.

Correlations between the capture locations of juvenile males and females were very high, as were the correlations between juveniles and adult females. This is not unexpected since young juveniles can be expected to remain in their natal area for some time before dispersing. Correlations between capture sites of adult males and juveniles were much lower.

Environmental correlates

Several environmental variables showed significant correlations with the pattern of water vole catches. Multivariate methods showed that between 55 % (adult male) and 79 % (adult female) of the variance of captures could be accounted for by these variables. This is a similar or higher level than that reported for *Microtus pennsylvanicus* (GRANT and MORRIS 1971).

Environmental variables correlated positively with water vole captures included water depth at 100 cm, and the presence of *Urtica dioica*, *Phragmites communis* and Gramineae indet. while negative variables were largely those associated with shallow water (large bank depth, *Polygonum amphibium*, *Sparganium erectum*, and *Phalaris arundinacea*).

Vegetation may provide food or cover or both, and different methods of measuring the vegetation will focus on these different aspects. A physiognomic approach will provide structural information emphasizing the importance of cover while a floristic approach gives information on the relative abundance of dietary species and their contribution to cover must be inferred from knowledge of their growth form. The latter approach was used here.

Plant species positively associated with water voles were all important food items. HOLISOVA (1970) examined stomach contents of water voles trapped on the edge of a shallow lake and found that *Phragmites communis* was the most frequently consumed species, clearly preferred over other emergent macrophytes, *Typha* spp. BOYCE (1991) also records *Phragmites* as an important food item and this was supported by observations on the study area. *Urtica* has also been regularly recorded as an important food item for water voles (HOLISOVA 1965; ASHBY and VINCENT 1976; WOODALL 1978).

The category "Gramineae indet." referred to areas where the grass had been grazed short ("lawns") and, lacking flowers or extensive leaves, could not be identified to species. Such areas were significantly correlated with captures of adult females in particular, and are recognised as distinctive signs of water voles' presence (STODDART 1977). The negative correlation between *Cirsium arvense* and juvenile water vole captures may reflect avoidance of the plants' protective spines by the juveniles.

Many of the environmental variables may be important in allowing water voles to evade predators. This study provided no direct evidence on the type or level of predation experienced by this population although several animals were caught with part of their tails bitten off, but in the literature there are many reports of the wide variety of mammals, birds and even fish that will attack water voles (SOUTHERN 1964; HOWES 1979; BOYCE 1991).

Smaller rodents are able to reduce predation either by being nocturnal or by remaining under cover while active. BIRNEY et al. (1976) have shown the importance of cover to *Microtus* populations, especially when at high density. The large size of the water vole (up to $10 \times$ the mass of *Microtus*) may preclude it from using vegetation as cover except in those localities, such as rivers, where the vegetation grows very dense and remains so for most of the year. LAWTON and WOODROFFE (1991) found that relatively high layering of the vegetation was associated with core areas and suggested that this might allow water voles to remain hidden from predators while foraging out of the water. Some of the plants identified as positively correlated with water vole catches in this study (*Phragmites* and *Urtica*) grew in dense clumps and so provided both food and cover. Howes (1979) gives three instances of where the removal of waterside vegetation led to a higher frequency of water vole remains in fox scats or barn owl pellets.

An important alternative escape mechanism of the water vole is to dive off the bank and then to swim away, entering an underwater tunnel or emerging some distance away (ZEJDA and ZAPLETAL 1969; STODDART 1977; pers. obs.). This is clearly facilitated by deep water because if the water vole dives into shallow water it may still be caught by the predator (e.g. a heron). Water depth at 100 cm from the bank had the highest correlation with water vole catches of any abiotic variable considered in this study indicating the importance of this feature. In Sweden, water voles are more terrestrial and also constitute a much higher proportion of weasels' diet (ERLINGE 1975) than they do in Britain (KING 1991).

Even the cover provided by dense clumps of emergent *Sparganium*, *Phalaris* and *Juncus* in sections 5, 6, 7, 11 and 12 were little frequented by water voles. Although these plants are all eaten by water voles (HOLISOVA 1965, 1970; WOODALL 1978; HOWES 1979), they are not preferred species (pers. obs.) and their association with shallow water probably made the sections unattractive to the voles.

LAWTON and WOODROFFE (1991) noted the importance of steep bank angles but did not specifically measure water depth and K. R. ASHBY (pers. comm. in BOYCE 1991) has remarked on the importance of deep water. High banks and steep bank gradients were not favoured by water voles in this area possibly because in some sections erosion and collapse of the banks led to shallow water off-shore.

The variables identified as important in this study have also been recognised in earlier more qualitative studies. ZEJDA and ZAPLETAL (1969) obtained similar results from a study of water voles in Central Moravia where they reported that a high bank, covered with "grass, ruderal or littoral vegetation" but not wooded, and deep water were all favourable to water voles. GAISLER and ZEJDA (1974) in a study of water voles on a pond, obtained their highest catches from trap stations "near slopy banks, covered with grass stands and neighbouring with fields and, at the same time, with luxuriant vegetation at the water's edge".

The variables that characterised the core sites in LAWTON and WOODROFFE'S (1991) study (a high percentage of grass, steep bank angles, and relatively high layering of the vegetation) were similar to those identified as important in this study, although the need to consider water depth in addition to bank heights and gradients was identified. The similarity in these results from studies conducted in different locations, on different sizes of rivers and with differing levels of predation gives some assurance that the key factors determining water vole distribution have been identified.

P. F. Woodall

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Zusammenfassung

Verteilung und Habitatwahl der Schermaus (Arvicola terrestris) an der Themse

An einem 1,6 km langen Uferabschnitt der Themse bei Oxford, England, wurde die Verteilung von Schermäusen zwei Jahre lang untersucht. Die Tiere traten stellenweise gehäuft auf; dies galt am deutlichsten für adulte Weibchen, weniger für Jungtiere und am wenigsten für adulte Männchen. Das Flußufer wurde in 32 Abschnitte von 50 m Länge eingeteilt. Daten über die Vegetation und Geomorphologie der Abschnitte wurden mit den Häufigkeiten von Schermausfängen in Beziehung gesetzt. Diese Analyse ergab, daß die Schermausfänge positiv korrelierten mit der Wassertiefe, mit dem Vorkommen von Urtica, Phragmites und Gräsern, und negativ mit der Uferhöhe, Uferbreite, Polygonum, Phalaris, Spargianum und Juncus. Alle bevorzugten Pflanzen dienen als Futter und bieten im Falle von *Phragmites* und *Urtica* auch Deckung. Flachwasser wurde gemieden, selbst wenn vorhandene Makrophyten Deckung boten. Tiefes Wasser erlaubt den Schermäusen vermutlich, möglichen Prädatoren durch Tauchen und Fortschwimmen zu entkommen.

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